REGENERATION AND LIABILITY TO INJURY.

T. H. MORGAN.

It is not uncommon to meet with the statement that there exists a relation between the power of regeneration of a part and its liability to injury. Certain well-established facts in regard to the regeneration of internal organs are entirely overlooked or disregarded in the attempt to show that the above relation "explains" the origin of regeneration. It would be interesting if those who hold that "there is no such thing as a general power of regeneration; in each kind of animal this power is graduated according to the need of regeneration in the part under consideration," — it would be interesting if such persons would show how such a thing could arise by means of "variation" and "survival of the fittest."

True, Weismann has given rather an elaborate explanation of his view of the matter; but I cannot believe that the chapter on regeneration in the Germ-Plasm will convince any one that the phenomena are in any way explained. For myself, I fail to see by what nice mechanism the power of regeneration is graduated according to the need of regeneration of each part. The "Natur-philosophie" seems not yet dead.

The following pages contain an account of some experiments made at Woods Holl, Mass., at the Marine Biological Laboratory during the summer of 1897, on the power of regeneration of the different appendages of the common hermit crab (*Eupagurus longicarpus*). A part of the animal is protected by the appropriated shell of a mollusc, and the appendages are modified in connection with the peculiar habitat of the animal. The anterior appendages are exposed, and some of them are not infrequently lost; while the appendages protected by the shell do not seem to be often injured. The results are treated under the following headings:

I. *Description of the Appendages.*

II. *The Percentage of Appendages Lost under Natural Conditions.*

III. *Experiments on Regeneration.*

IV. *Conclusions.*

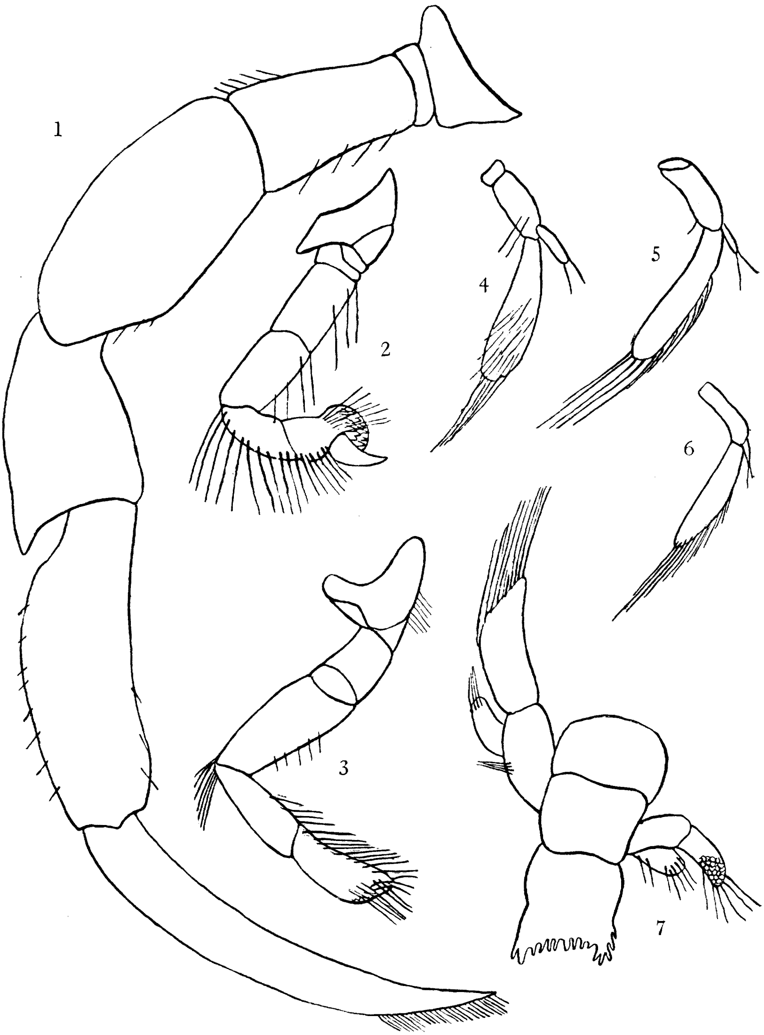


FIG. 1. Third pair of walking legs. — FIG. 2. Next to last thoracic leg. — FIG. 3. Last thoracic leg. — FIG. 4. First abdominal appendage of male (belonging to second segment). — FIG. 5. Second abdominal appendage of male. — FIG. 6. Third abdominal appendage of male. — FIG. 7. Telson and sixth segment with last pair of abdominal appendages.

I. Description of the Appendages.

The eyes, antennae, antennules, and mouth parts (maxillae and maxillipeds) are not sufficiently different from those of other Decapoda to call for special comment. The first three pairs of walking legs are large and strong (Fig. 1), and protrude from the shell when the animal moves about.

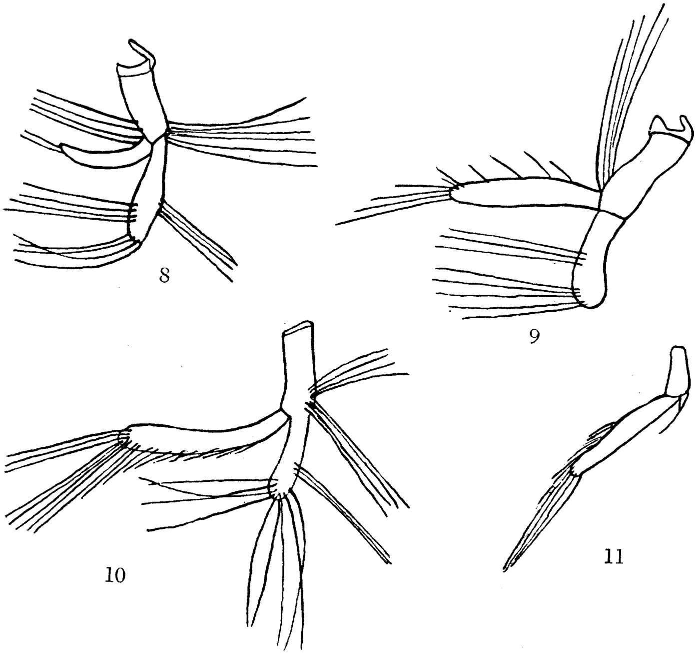


Fig. 8. First abdominal appendage of female (belonging to second segment). — Fig. 9. Second abdominal appendage of female. — Fig. 10. Third abdominal appendage of female. — Fig. 11. Fourth abdominal appendage of female (= third abdominal appendage of male). (Same scale as last figures.)

The fourth (Fig. 2) and fifth (Fig. 3) pairs of legs are small and weak. They are brought to the edge of the shell when the crab is active, but take no part in locomotion. They may be of service in bracing the animal against the shell.

The anterior abdominal appendages are entirely absent on one side of the body, — the side toward the axis of the shell. Those on the other side are said to represent in the female the second, third, fourth, fifth, and sixth appendages (Figs. 8, 9,

10, 11, and Fig. 7). In the male the anterior abdominal appendages are smaller (Figs, 4, 5), and only the second, third, fifth, and sixth appendages are present. The abdominal appendages of the female (second, third, and fourth) carry the eggs during the breeding season. These appendages are supplied with long hairs, to which the eggs are attached. In the male the hairs are not so well developed.

The last abdominal appendages (Fig. 7) are hard and strong — the left one much larger than the right. These appendages seem to play an important part in anchoring the abdomen in the shell. So securely is the abdomen fastened that it will often pull apart before the appendages loosen their hold.

Are any of these appendages rudimentary? A statement that this or that part is rudimentary implies a knowledge of the descent of the animal possessing such structures. A simple reduction in size, moreover, is not a criterion, because a smaller appendage may be in certain cases a more perfect adaptation than a larger one. For instance, most zoölogists would admit, I think, that the fourth and fifth pairs of thoracic legs of the hermit crab have been reduced in size, but how far this reduction is due to degeneration and how far to new adaptation is difficult or impossible to say. In comparison with most other Decapoda these appendages seem reduced, and they have lost their locomotor function.

In the abdominal region the evidence in favor of a reduction or rudimentary condition of the appendages of the male is stronger. On one side the appendages have entirely gone, and on the other side they are small and weak, and the third appendage (on the fourth segment) has completely disappeared. In other related forms the two anterior abdominal appendages of the male have also entirely gone, or are represented by only a few tufts of hairs.

The terminal appendages, on each side of the telson, do not appear reduced in comparison with the similar appendages of other Crustacea, but one is nearly twice the size of the other (Fig. 7).

II. The Percentage of Appendages Lost under Normal Conditions.

The anterior end of the body is exposed when the crab is moving about. This portion of the body is covered by a thick, hard cuticle. The parts enclosed in the shell are softer, excepting the telson and the sixth abdominal appendages. We should anticipate that the exposed portions of the body, despite their greater strength, would be more often injured, and such is the case. I have made an examination of a number of animals, and have found that quite often one of the first three pairs of walking legs has been lost. The antennae, too, are often broken at the end.

The first three thoracic legs can be thrown off near the basal joint. Autonomy is known to take place also in other Decapoda (see papers by Fredericq, Réaumur, Goodsir, Chantran, Brook, Andrews, Herrick). This has been looked upon as an adaptation for regeneration! The fourth and fifth pairs of thoracic legs cannot be thrown off.

The following observations show the percentage of individuals that have lost, under natural conditions, one or more appendages.

Of 47 individuals (collected June 12), 5 had lost one of the first three walking legs.

Of 73 individuals (June 14), 13 had lost one of the first three legs.

Of 68 individuals (June 17), 3 had lost one of the first three legs.

None of these were examined in respect to other appendages. If we reduce the figures given above to percentages, we find 10.6, 17.8, and 4.4 per cent, respectively. That is, out of 188 individuals, 21 (or 11 per cent) had lost an appendage.

In order to ascertain whether the other appendages were also lost, a hundred individuals were collected in September; they were killed and then removed from the shells, and all the appendages carefully examined. The following results were obtained:

The eyes were present and uninjured in all the individuals. The antennae and antennules were also present. In some cases the ends of the antennae were broken off. The third maxillipeds were present and uninjured. One of the chelae was absent or regenerating in five individuals, and one of these had lost both right and left chelae (6 per cent). A second leg was absent in one case (1 per cent), and a third leg in two cases (2 per cent). In all, therefore, 9 per cent had lost one of these legs. In not a single case were the fourth or fifth legs missing or injured.

In the abdominal region the third abdominal appendage (belonging to the fourth segment) was absent in one female, and in one male the second abdominal appendage (belonging to the third segment) was absent. In another male the broken proximal end of the second abdominal appendage was present, and in another the first abdominal appendage was reduced in size, and the second also was smaller than the normal, but the third appendage (representing the fifth segment) was normal. The two cases — one male, the other female — where an appendage was absent may be the result of individual variation; although it is also possible that the appendage was accidentally pulled off in removing the crab from the shell. In the latter case some evidence of tearing or breaking ought to appear, but no such evidence was found. The individual in which the first and second abdominal appendages are smaller than normal may be the result either of variation or of incomplete regeneration. The evidence, therefore, furnished by an examination of the abdominal appendages is conflicting, and it is possible that the appendages may be occasionally lost.

The sixth abdominal appendages were present in all cases.

Forty of the individuals were females and sixty males.

Summary. — The results, taken as a whole, show that the first three walking legs are most often lost. The last two thoracic legs were not absent in a single case examined, and the same statement holds for the last abdominal appendages. The second (♂) and third (♀) abdominal appendages were absent in one case each, but whether from individual variation or from loss during life is not known. Yet, since in one case small

abdominal appendages were found, it may be that these appendages are sometimes lost.

Shall we find, then, in the regeneration of these different appendages any correspondence between the power of regeneration and the liability to injury or loss of a part?

III. Experiments on Regeneration.

Two series of experiments were made, — one lasting through parts of June and July and another in August and September.

The crabs, after the removal of one or more appendages, were kept in aquaria with running water. They were fed every day or two.

In the first series of experiments the following operations were made: From one series one or more of the walking legs were removed on June 12. On July 2 the ten crabs were killed and examined.

(1) The right and the left first legs were both beginning to regenerate. The tip of a second and of a third leg had been cut off, but had not regenerated.

(2) The right first leg had a new bud.

(3) The right first leg had a long new part.

(4) The left first leg had a moderately long new part.

(5) The right first leg, removed very close to body, had not regenerated, nor had the tips of the third and fourth legs that had been cut off.

(6) The right first leg and the third left leg had not regenerated (very small individual).

(7) The first right leg had a very little (if any) new tissue, and the left second leg had a long new part.

(8) The left second leg and the right second and third legs had long new parts.

(9) The left second leg had regenerated a small new part.

(10) The tip of the left third leg had not regenerated.

Summary. — In three cases the leg had not regenerated; in one of these the leg had been *cut off* very near to the body, and in the other two cases two legs of the same crab, presumably *thrown off* after injury, had not regenerated. Seven new legs

were forming, and three others had the beginning of a bud. In three cases in which the tip of the leg had been cut off no new part formed. As these legs were in constant use, any new tissue would, perhaps, even if it formed, be worn off.

From another series one of the last two thoracic legs or the first, second, or third abdominal appendage was cut off on June 12. On July 2 the crabs were killed and examined. Thirty-one individuals were present at the end of the experiment, and of these five were regenerating the fourth leg, and four showed as yet no signs of regenerating the lost leg; six were regenerating the fifth leg; three were regenerating the first abdominal appendage, but nine showed no signs of regeneration in this appendage; two were regenerating the second abdominal appendage (♂), and four were not regenerated (♂).

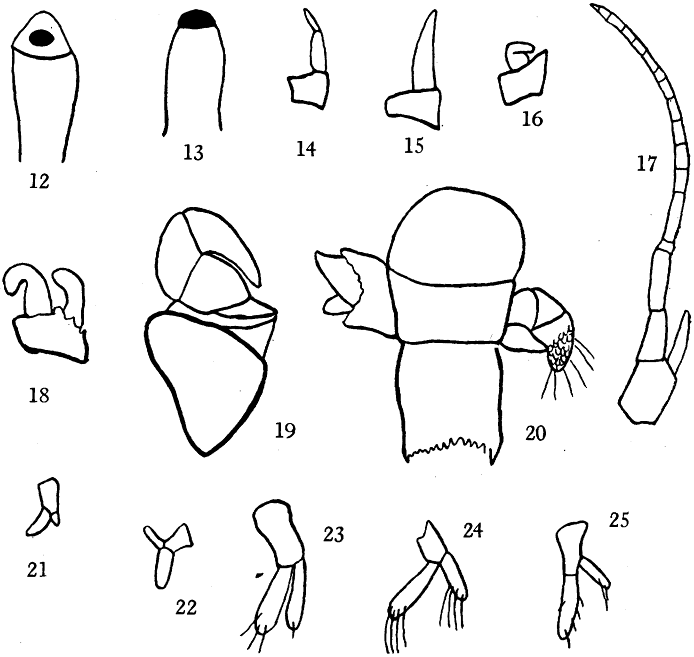
Summary.—The results show that the small fourth and fifth legs possess the power of regeneration. The abdominal appendages (first, second, and third) have also the power of regeneration, but the percentage of those in which the process takes place is smaller than in the case of the thoracic appendages. Whether this difference is due to the longer time necessary for these appendages to grow again or to some difference connected with the place at which they were cut off is not clear. Whether a molt is necessary for the reappearance of the abdominal appendages I do not know. It may be that they do more rarely regenerate, and this in turn may be connected in some way with the amount of food supply brought to the region from which they arise. At any rate, the positive result in those cases where regeneration took place shows that these appendages still possess the power of regeneration.

In another experiment one of the last abdominal appendages, the right or the left, was cut off on June 14. On July 2 all, with one exception, were regenerating. Eight individuals had a new, or regenerating, left appendage, and the right smaller appendage was regenerating in three cases. In a single case the absent right appendage had not regenerated.

In the second series of experiments, made on August 18 and brought to a close on September 15, the eyes, antennae,

antennules, and maxillipeds were cut off; and I also repeated the experiment of removing one or more of the first three or four (♀) abdominal appendages.

Eyes. — In ten individuals the pigmented tip of the eye was cut off, and in ten others the eye-stalk was cut off at or near



FIGS. 12, 13. Eyes regenerating from distal end of stalk. — FIGS. 14, 15. Antenna-like structures regenerating from base of old eye-stalk. — FIGS. 16, 17. Antennae regenerating. — FIG. 18. Maxilliped regenerating. — FIG. 19. First walking leg regenerating. — FIG. 20. Left last abdominal appendage regenerating. — FIGS. 21, 22. First and second abdominal appendages regenerating. — FIGS. 23–25. First, second, and third abdominal appendages of male regenerating. (Drawn to same scale as preceding figures.)

its base. Eight individuals that had the tip of the eye cut off were alive at the end of the experiment, and seven of these had a new pigment spot at the end of the old stalk (Figs. 12, 13). In some cases a sharply defined, oval, pigmented body was present, and two of these, when cut into sections, showed that a new eye was in process of development.

In the other ten individuals, in which the eye-stalk had been cut off near its base, five had regenerated a new part, and five had not; but in this experiment the new organ was antenna-like (Figs. 14, 15). Herbst also found that when the eyes of

Palaemon and Sicyonia were removed sometimes an eye and sometimes an antenna reappeared. Chantran, in 1873, also noticed that if half of the eye-stalk of the crayfish were cut off a new eye appeared. If the entire eye were excised, it was not regenerated. It is interesting to note that in the hermit crab the new eye came in when the stalk was cut off near its outer end, and an antenna-like structure appeared in five out of ten cases in which the stalk was cut off near its base.

Antennae.— Nine individuals had begun to regenerate a new antenna from the old basal joint. Five of these had long segmented antennae, one-half or one-fourth as long as the fully formed antenna (Fig. 17). Four of the nine had smaller buds, showing generally evidences of segmentation (Fig. 16). Only one of the ten survivors had not regenerated at all.

Antennules. — One had completely regenerated; two, on the same individual, were two-thirds the full length; three had new short buds, and one of these individuals had also lost the other antennule, but had not regenerated it. A sixth individual had not regenerated. Four individuals died during the time of the experiment.

Maxillipeds. — The third and sometimes the second maxilliped were cut off from one side. In all eight survivors (of ten operated upon) the parts removed had begun to regenerate. In two cases the third maxilliped was nearly as long as the normal appendage. In five cases it was represented by two small outgrowths from the basal joint (Fig. 18). In one individual a very short bud was present. The second maxilliped had been cut off in five of the above cases. In four individuals it was represented by two new processes growing out of the basal joint. In one case the new maxilliped was half the normal size. A part of the first maxilliped had been cut off in one instance and was regenerating.

Abdominal Appendages. — Of twenty-four individuals from which the abdominal appendages had been cut off, fourteen were alive on September 15. Only two had regenerated the first abdominal appendage (Figs. 21, 23); while ten other individuals from which the same appendage had been cut off had not regenerated. Two had not had this appendage cut off.

Two individuals (the same that regenerated the first appendages) regenerated the second appendages (Figs. 22, 24). Both were males. Eleven others had not regenerated. The third abdominal appendage of a male (belonging, therefore, to the fifth abdominal segment) had regenerated (Fig. 25). This was also on one of the individuals that had regenerated the first two appendages. The same appendage had been removed from six other males and from two females, and had not regenerated. In three cases the third abdominal appendage (of the fourth segment) of three females had been removed and had not regenerated.

How far the regeneration of these appendages is dependent on an ecdysis I do not know. The more anterior appendages of the body may develop quite far before the animal changes its exoskeleton.

Summary. — The experiment shows that the abdominal appendages have the power of regeneration, although they do not regenerate as readily as do the more anterior appendages, or as do the last abdominal appendages. The positive evidence showing that the anterior abdominal appendage regenerated in several cases is, I think, of much greater weight than the negative evidence that they did not do so as frequently as the other appendages during the short time of the experiment.

In regard to the relative usefulness of the abdominal appendages little can be said. In the male they are small and weak, and one, the third, present in the female, is absent in the male. In the female the first three abdominal appendages carry the eggs. They are, therefore, essential for the existence of the race; yet there is no difference found between the power of regeneration of the three anterior egg-bearing appendages of the female and the two corresponding appendages of the male.

IV. Conclusions.

The results of the experiments show that the more anterior appendages regenerate quickly. A large percentage of the parts removed had begun to regenerate even during the short

time of the experiment. An examination of the frequency of loss of the appendages showed that from 9 to 11 per cent of the crabs living under natural conditions had lost one of the first three pairs of walking legs. The eyes, antennules, maxillipeds, and especially the two last pairs of thoracic legs do not seem to be often injured, at least, not in all the individuals that I have examined. Nevertheless, these parts regenerate as quickly and in as large proportion as the three walking legs. Moreover, the last abdominal appendages that are used to hold the abdomen in the spiral shell regenerate as readily as the more exposed anterior appendages. It is improbable that these strong, hard appendages on the end of the soft abdomen can be often injured inside the smooth shell; and when changing shells the crabs take great precaution to expose the abdomen as little as possible. In no cases of the hundred individuals examined, and in none of the other individuals that have passed through my hands, have I found these appendages injured or missing. It is, therefore, of some importance to find that these appendages regenerate quickly, and in as large proportion as the thoracic legs.

The abdominal appendages have disappeared on one side in both sexes, and those on the other side that remain have shifted their position high up on the abdomen. In the male the appendages (particularly one of the branches) are smaller than in the female, and the third appendage of the female has disappeared in the male. Since the eggs are carried by the anterior abdominal appendages of the female, these must be essential to the existence of the species; yet in the experiment these appendages did not regenerate oftener in the female than in the male.

The question of the degeneracy, and at the same time of the uselessness, of a part is fraught with difficulty, for we have, in the first place, very little evidence (and that little rests only on probability) as to whether a part has been reduced during the evolution of the species; and, in the second place, we cannot tell, even if a part be admitted to be reduced in size, of how much use such a part may still be to the animal. Therefore, although we find the last two pairs of thoracic legs and the

anterior abdominal appendages of the male still capable of regeneration, we do not know with certainty that the parts are degenerate. The question is further complicated by the amount of food material that is brought to the part of the body from which the appendage springs. If the amount is small, we can readily imagine that the regeneration may be retarded, or not even started, although the cells might be potentially capable of regenerating the missing part. It is not improbable that the smaller 'reduced' appendages would be most likely to suffer in this respect.

There is still another factor that must be taken into account, *viz.*, the place at which the appendage is cut off, for it is probable that, while an appendage may regenerate at one level, it may not be able to do so at another. Perhaps, for instance, had the abdominal appendages been cut off nearer to the body, a larger or smaller percentage would have regenerated.

In regard, however, to the problem of the frequency of injury of a part and its capability to regenerate, the preceding results, I think, speak with sufficient clearness. No such relation is found to exist. The advocates of such a view overlook a very vital part of the problem. If, for instance, it were found, as the result of a large number of observations, that those animals or parts of animals that were most subject to injury had most highly developed the power to regenerate lost parts, it would by no means follow, as Weismann and other Darwinians claim, that this result must have come about by what they call a process of natural selection. They overlook the possibility that unless these animals had from the beginning the power to regenerate they could not continue to live under the adverse circumstance. The animal would be then either entirely destroyed or else confined to other locations where the danger did not exist. Many persons confuse this statement with the theory of natural selection, but the two views are as wide as the poles apart.

We need not, perhaps, be greatly concerned with the argument that attempts to make plausible a connection between accidental injuries and the power of a part to regenerate, for there are known already a number of remarkable cases of

regeneration of internal organs, and these organs can rarely or never be injured. If, then, such organs have the power of complete regeneration, why need we seek for special explanations for those cases in which the organs happen to be more or less exposed to injury?

BRYN MAWR COLLEGE, BRYN MAWR, PENN.,
January 15, 1898.